Research Highlights

- Forest patch size and palm density predict the occurrence of *Alouatta belzebul* in Amazonian savannas.
- Flooded forests may be a keystone habitat for *A. belzebul* in small forest patches.

The occurrence of the red-handed howler monkey (*Alouatta belzebul*) in Amazonian savannas is related to forest patch area and density of flooded area palms

Short title: Predicting the occurrence of howlers

Saulo M. Silvestre[1], Joanna M. Setchell[2], Bayron R. Calle-Rendón[1], José J. de Toledo[1] and Renato R. Hilário[1,3,4]

[1] Postgraduate Program in Tropical Biodiversity, Federal University of Amapá, Brazil.

[2] Department of Anthropology, Durham University, Durham, UK.

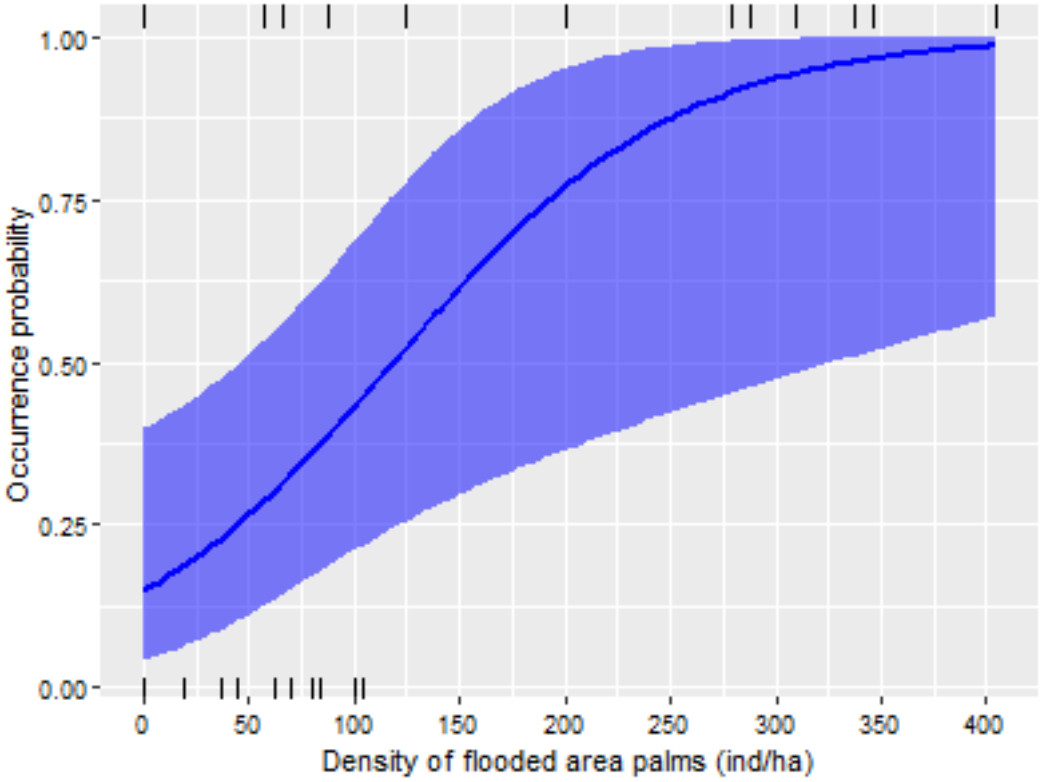
[3] Postgraduate Program in Environmental Sciences, Federal University of Amapá, Brazil.

[4] Faculty of Sciences, University of Lisbon, Portugal

Corresponding author: Saulo M. Silvestre. Programa de Pós-graduação em Biodiversidade Tropical, Universidade Federal do Amapá, Rod. Juscelino Kubitschek, S/N, Jardim Marco Zero, Macapá-AP, 68903-419, Brazil. E-mail: saulomsilvestre@gmail.com. Phone: +55 (96) 99141-9930.

Abstract

All Neotropical primates are arboreal and thus depend on forests for their survival. This relationship put many Neotropical primates at risk of extinction due to the high rates of deforestation in the tropics. We assessed the influence of vegetation structure and forest patch attributes on the occurrence of the threatened red-handed howler monkey (*Alouatta belzebul*) in an Amazonian savanna. Using a sample of 38 forest patches in a region of ~2,000 km² in the state of Amapá, northern Brazil, we used logistic regression to find the best predictors of the occurrence of *A. belzebul*. We assessed patch area, patch isolation, the proportion of seasonally flooded forest in the patch, the density of flooded area palms, forest height, canopy cover, and diameter at breast height of trees. Patch area and palm density were the best predictors of the occurrence of *A. belzebul* in forest patches, both having a positive effect on the probability of occurrence. Our results indicate that areas of flooded forest in forest patches may be keystone habitats for *A. belzebul* living in Amazonian savannas. The observed effect of palm density on *A. belzebul* suggests that this variable is useful for planning conservation actions, including the selection of areas for protection and management strategies for areas inhabited by this primate.



Keywords: *Alouatta belzebul*, Amapá, Palms, Forest structure, Flooded forest, Patch occupancy

Introduction

The factors that have the greatest influence on species occurrence are key to the selection of high-quality areas for the conservation of threatened species, and the development of management strategies to reduce their probabilities of extinction. Arboreal primates in fragmented landscapes only occasionally travel among forest fragments, mostly to migrate between groups (Mandujano, Escobedo-Morales, & Palacios-Silva, 2004; but see Pozo-Montuy & Serio-Silva, 2007). The habitat variables affecting their occurrence may help to explain their distribution in the landscape and guide the selection and management of areas for conservation that optimize the probability of long-term survival of local populations (Arroyo-Rodríguez & Dias, 2010).

The size of forest fragments or patches and edge effects are often major factors in determining the diversity and quantity of resources available for primates (Arroyo-Rodríguez & Mandujano, 2006; Estrada & Coates-Estrada, 1996). Habitat heterogeneity may also reduce the risk of food scarcity if different habitats have asynchronous peaks in productivity (Defler & Defler, 1996; Stevenson, 2016). For example, adjacent flooded forests can be key to the survival of primates in unflooded forest fragments during times of food scarcity, thanks to their different floristic composition and complementary phenology (Ahumada, Stevenson, & Quiñones, 1998; Carretero-Pinzon & Defler, 2019).

Among Neotropical primates, howlers (*Alouatta* spp.) are remarkably resilient to habitat disturbance, thanks to their ecological flexibility, and especially their flexible diet (Peres, 1997). Howlers can include exotic species in their diet (Bicca-Marques, 2003) and survive on an almost entirely folivorous diet during lean periods (Pavelka & Knopff, 2004). They may also survive in small (<5 ha) forest fragments, helping them to cope with forest fragmentation (Bicca-Marques, Chaves, & Hass, 2020; Rodriguez-Toledo, Mandujano, & García-Orduña,

2003). However, fragmentation has potentially negative effects on howler populations, which may include reduced food availability in the small fragments and higher levels of physiological stress, competition, parasite load, and hunting pressure (Arroyo-Rodríguez & Dias, 2010; Rimbach et al., 2013).

In the Amazon, floodplain (Várzea) forests have the most abundant populations of howlers, as a result of the high levels of forest heterogeneity and soil fertility found in this habitat (Peres, 1997). In fragmented landscapes, forest area is often the main determinant of howler occurrence (Arroyo-Rodríguez & Dias, 2010). Measures used as proxies for food availability, like the density of large trees and total basal area, also play a particularly important role in the occurrence and population densities of howlers in small fragments (Arroyo-Rodríguez, Mandujano, Benítez-Malvido, & Cuende-Fanton, 2007; Hue, Caubet, & Moura, 2017). While vegetation parameters like canopy cover, mean size of trees, and forest height are often interpreted as positively correlated with habitat quality for howlers (*e.g.* Bolt et al. 2019), their effects may be more easily detected on population parameters (i.e. abundance) than occurrence (Anzures-Dadda & Manson, 2007). However, by positively affecting primate abundance, a given driver may also contribute to population persistence, thus affecting primate occurrence indirectly.

The red-handed howler monkey (*Alouatta belzebul*) is an endemic threatened (Vulnerable) primate from Brazil (Montenegro et al., 2019). Habitat loss and hunting are the main threats to this species and have resulted in the local extinction of several populations (Montenegro et al., 2019). *A. belzebul* faces deforestation and habitat fragmentation in most of its geographic distribution, i.e. in the Atlantic Forest and the arc of deforestation in the Amazon (Montenegro et al., 2019). The least degraded region of its distribution is in the southeast of the

state of Amapá, North of the Amazon River. However, this region has suffered increasing anthropogenic impacts in recent years (Hilário et al., 2017; Mustin et al., 2017).

The landscape of southeastern Amapá where *A. belzebul* occurs is predominantly composed of lowland (Várzea) forests, flooded fields, and savannas. The savannas are characterized by open formations, permeated by gallery forests and forest patches subjected to varying flooding intensity, from patches that are completely dry land to patches that are entirely floodable (IEPA, 2008). This ecosystem covers ~10,021 km² of Amapá, but over 1,000 km² has already been lost to eucalyptus plantations and it faces imminent threats mainly due to the accelerated expansion of agribusiness in the state, which is replacing remaining savannas with soybean plantations (Hilário et al., 2017). Changes in the matrix often result in changes inside forest fragments, including forest structure and food availability (Fischer & Lindenmayer, 2007). In this context, understanding how variation in habitat structure influences the occurrence of *A. belzebul* is a key aspect of conservation planning.

In this study, we investigated the influence of patch attributes (area, isolation, the proportion of the patch that is seasonally flooded), and vegetation structure (forest height, canopy cover, tree DBH, and density of flooded area palms) on the probability of occurrence of *A. belzebul* in forest patches in the savannas of Amapá. We hypothesized that *A. belzebul* occurrence would be related to habitat availability and quality. Specifically, we predicted that patch area, forest height, canopy cover, and tree diameter would be positively associated with *A. belzebul* occurrence. Conversely, we predicted that patch isolation would be negatively associated with *A. belzebul* occurrence. We also hypothesized that seasonally flooded areas would have positive effects on *A. belzebul* occurrence because they represent potential sources of food that may complement what is available in unflooded portions of the forest patches. Because not all flooded portions of the forest patches in our study region are forest (i.e., with

dicot trees), we used both the proportion of the patch that is seasonally flooded, which does not take into account the type of vegetation, and the density of flooded area palms, as an indicator of flooded forests. We predicted that intermediate levels of these two variables would have positive effects on *A. belzebul* occurrence, because while smaller areas of seasonally flooded forest would be an advantage, the occurrence of howlers will start to diminish again at much larger proportions of flooded forest, due to the lack of unflooded forest.

Methods

Ethics statement

This research complied with the American Society of Primatologists' Ethical Principles for the Treatment of Non-Human Primates and with Brazilian Ethical Standards for research with animals, and adhered to all Brazilian legal requirements.

Study region

The Brazilian state of Amapá has a humid tropical climate of type Am according to Köppen and Geiger's classification system (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006). The year is characterized by two seasons: the rainy season runs from December to July, with average monthly rainfall ranging between ca. 200 and 400 mm; and the dry season, from August to November, with average monthly rainfall of less than 100 mm (IEPA, 2008). The savanna region is characterized by grasslands with sparse trees and dense herbaceous/shrub strata. In the landscape, gallery forests, stands of buritis (*Mauritia flexuosa*), and forest patches stand out amidst the predominantly open formations (IEPA, 2008).

In the Amapá savannas, *A. belzebul* is concentrated in the municipalities of Santana and Macapá. Park savanna and grass savanna formations predominate in this region (Mustin et al., 2017). This is also the region with the highest human population density in the state, with a metropolitan region (~646,000 inhabitants) that includes Macapá, Santana, and Mazagão (IBGE, 2017a; Mustin et al., 2017). The recent expansion of soybean plantation areas in the state is also concentrated in this region (IBGE, 2017b), making this currently the region with the greatest pressure on biodiversity in Amapá.

Selection of forest patches

We defined forest patches as areas of ≥1 ha of native forest that were not structurally connected to other forest patches (Dias, Alvarado-Serrano, Rangel-Negrín, Canales-Espinosa, & Cortés-Ortiz, 2013; Puig-Lagunes, Canales-Espinosa, Rangel-Negrín, & Dias, 2016). Given the scarcity of information on the distribution of *A. belzebul* in the region, we selected 126 patches (≥1 ha) for a preliminary survey of the occurrence of the species through interviews with residents of the region and obtained information for 58 of these forest patches in February, October and November 2017. We then selected 38 forest patches as our sample: half with indications of presence of *A. belzebul* and the other half with no indication of their presence (Figure 1). We carried out playback sampling in 22 of these patches to confirm the information from the interviews (Calle-Rendón, Toledo, Mustin, & Hilário, 2020). In the remaining 16 patches, we confirmed the presence of the species via opportunistic records during vegetation sampling.

The playbacks were conducted using a Max Print 601205-3 speaker (frequency range: 50 to 20,000 Hz, output power: 100 RMS) in points defined by transects of 800 m. We broadcast vocalizations of *A. belzebul* at the beginning and the end of each transect at 07:00 a.m. and 4:40 p.m., respectively. In the meantime, the researcher walked the transect actively looking for the

howlers. We sampled one transect per day. The number of transects was defined by the patch area as follows: ≤25 ha: 2 transects; >25-50 ha: 3 transects; >50-100 ha: 4 transects; and >100 ha: 5 transects. If the size and/or shape of the patch did not support one transect of 800 m, the quantity and length of transects were adjusted accordingly, so the minimum distance between points was 200 m. We confirmed the presence of *A. belzebul* by direct (visual and auditory) and/or indirect (feces) signs in all 19 patches with indications of its presence. We found no evidence of howlers in any of the 19 patches where respondents said they were absent. Data collection in forest patches was carried out from July 2018 to April 2019.

In the study region, *A. belzebul* inhabits forest patches and gallery forests originally embedded in open savanna formations (i.e. park savannas and grass savannas), flooded fields, and lakes. Now the landscape also includes human settlements and activities that changed or replaced the matrix in some areas (i.e. soybean and eucalyptus plantations). These changes may indirectly affect the local distribution of *A. belzebul* through changes in variables like matrix permeability or hunting pressure. However, the matrix surrounding our sampled forests was predominantly composed of natural habitats, mostly open savanna formations. All forest patches had potential migration routes to/from other forested areas that did not include human-made landscape features, except for eventual dirt roads. Only one forest patch had direct contact with an urban area.

Sampling of forest patches

We evaluated patch area, patch isolation, the proportion of the patch that is seasonally flooded in the patch, the density of palms typically abundant in flooded forests (palm density), mean forest height, mean canopy cover, and mean diameter at breast height (DBH) of trees with ≥10 cm DBH for each forest patch.

175 Forest patches in Amazonian savannas are often partially seasonally flooded. In our study
176 region, we can separate the flooded portions of the forest patches into two general forms: (i)
177 forests formed by trees and arborescent palms, and (ii) herbaceous/shrubby clearings with
178 higher flooding intensity, dominated by dense tufts of atuíras (*Machaerium lunatum*) or arumãs
179 (*Ischnosiphon polyphyllus*) and sparsely distributed *M. flexuosa* palms. The former presumably
180 provide more advantages for howlers (*e.g.* support for locomotion, shelter, and food sources)
181 than the latter. These different forms result from different flooding intensities. Areas that are
182 flooded for longer periods tend to be more similar to flooded fields, while areas flooded for
183 shorter periods include a higher density and richness of palms and tree species. We addressed
184 this habitat difference by assessing the effects of flooded areas using two variables: the
185 proportion of the patch that is seasonally flooded, and the density of flooded area palms. We
186 used the density of palms (*E. oleracea*, *M. flexuosa*, and *M. armata*) to assess the extent of
187 flooded forest because Arecaceae is often the most abundant plant family in flooded forests
188 (Aquino & Bodmer, 2004), and because of the ease in identifying them in the field.

189 We calculated the patch area and the shortest distance to the nearest forest patch (i.e.
190 patch isolation) based on satellite images from Google Earth Pro (version 7.3.2.5776). We
191 calculated the mean forest height for each patch using Synthetic-Aperture Radar (SAR) images
192 (res: 2.5 m x 2.5 m) of the vegetation height (created using pulses that are reflected by the
193 vegetation), using all cell values ≥5 m, thus excluding clearings or imperfections in the
194 definition of the polygons that could include the savanna matrix. We estimated the proportion
195 of the patch that was seasonally flooded using SAR images (res: 2.5 m x 2.5 m) of the altitude
196 (created using pulses that are reflected by the ground), by calculating the proportion of cells
197 with altitudes ≤ 5 m.

198 We measured the remaining variables using 100 m x 2 m plots. We determined the
199 number of plots per forest patch using the patch area (≤ 15 ha: 4 plots; >15-25 ha: 8; >25-50
200 ha: 12; >50-100 ha: 16; > 100 ha: 20). We chose the starting point of each plot using stratified
201 random selection. We created a grid (200 m x 200 m) covering each of the patches using the
202 'raster' package (Hijmans, 2017) in R software (R Core Team, 2017) and randomly sampled
203 points, conditioned to a maximum of one point per grid cell. We determined the orientation of
204 the plot in situ, avoiding abrupt changes in altitude and preferably pointing towards the starting
205 point of the next plot. It was not possible to sample the intended number of plots in some forest
206 patches due to limitations in size (some patches were too small) or shape (some irregular shapes
207 limited the number of plots that could fit inside the patch). The total area sampled per forest
208 patch varied from 0.06 ha to 0.40 ha, and the percentage of sampled area per forest patch varied
209 from 0.11% in the largest (228.5 ha) to 3.30% in the smallest (1.8 ha) patch.

210 To estimate canopy cover, we obtained hemispheric photographs using a fisheye lens
211 (180º) attached to a smartphone, 1.5 m from the ground at three equidistant points, forming a
212 triangle with sides of 5 m, every 25 m within the plots (Tichý, 2016). Using the GLAMA
213 software (Gap Light Analysis Mobile Application), we calculated the Modified Canopy Cover
214 index (Modif. CaCo) for each photograph. This index describes the proportion of the
215 photograph represented by vegetation (canopy), correcting for distortion (Tichý, 2016). We
216 measured the diameter at breast height (DBH) of trees, and counted and identified all palms at
217 least 2 m tall within the plots. We calculated the palm density (palms/ha) by dividing the total
218 number of *E. oleracea* clumps, *M. flexuosa*, and *M. armata* by the area sampled (ha) in the
219 patch.

220 The number of forest patches in each size class varied, with nine patches of ≤15 ha, 10 of
221 >15-25 ha, eight of >25-50 ha, six of >50-100 ha, and five of >100 ha. The mean modified

canopy cover index of the sample patches varied from 75% to 84%, except for one forest patch with an exceptionally discontinuous canopy (61%) due to a large number of felled trees (Table 1). Except for forest height and mean tree DBH (r = 0.62), our variables were weakly correlated (r = 0.31-0.34) (Table 2). Patch isolation varied from 10 m to 288 m and 84% (n = 32) of the forest patches were less than 200 m from the nearest neighboring forest.

Data analysis

We used R software for all analyses (R Core Team, 2017). We used a logistic regression model to determine the influence of vegetation structure parameters (mean forest height, mean canopy cover, mean DBH of trees, palm density) and patch attributes (area, patch isolation, and the proportion of the patch that was seasonally flooded) on the occurrence of *A. belzebul*. We included a quadratic term for the proportion of the patch that was seasonally flooded and palm density in our model, because we predicted a non-linear relationship between those variables and the occurrence of *A. belzebul*. However, this drastically decreased the quality of the models, so we removed the quadratic terms. We used the function 'model.avg' in the package 'MuMIn' (Barton, 2018) to compare the models with all possible combinations of predictors and ranked them from best to worst, based on the lowest to highest AICc (Akaike Information Criterion corrected for small samples). We used the R package 'gam' (Hastie, 2020) to create a Generalized Additive Model (GAM) applying a local regression smoother (LOESS) function to the palm density to assess the relationship between this variable and the occurrence of *A. belzebul* in the best logistic model (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Logistic regressions assume perfect detection, which is difficult to ensure in most field scenarios. Other, more expensive and time-consuming analytical approaches such as occupancy models could give us better results. However, by using multiple approaches to obtain occurrence data (i.e. interviews, playback, active searches, and opportunistic records), we found

246 evidence of the presence of howlers in all patches where interviewers indicated its presence and
247 we did not find evidence of their presence in any of the patches where interviewers indicated
248 its absence. Thus, the low probability of false absences in our dataset warrant the use of logistic
249 regression models.

250 We tested the models for multicollinearity using the variance inflation factor (VIF –
251 Quinn and Keough 2002), with the 'car' package (Fox & Weisberg, 2011). None of the
252 variables had VIF > 3, indicating no problems of multicollinearity (Zuur et al., 2009). The
253 'outlierTest' tool in the 'car' package found no significant influence of outliers on the model.
254 Finally, there was no spatial autocorrelation of the regression residuals, as indicated by
255 variograms made with the 'gstat' package (Pebesma, 2004).

256 **Results**

257 The best model predicting the distribution of *A. belzebul* in the forest patches included
258 only patch area and palm density, with the lowest AICc and an Akaike weight almost 3 times
259 higher than the second-best model, which included canopy cover (Table 3). Furthermore, both
260 patch area and palm density were included in the 15 best models. None of the other vegetation
261 structure parameters (mean forest height, mean canopy cover, and mean DBH of trees), or patch
262 attributes (patch isolation and proportion of the patch that is seasonally flooded) were important
263 predictors of the probability of *A. belzebul* occurrence. Forest patch area had the strongest effect
264 on the probability of occurrence of *A. belzebul*, which varied from < 10% in patches below 10
265 ha to almost 100% in patches larger than 100 ha (Figure 2). Palm density also had a positive
266 influence on the probability of occurrence of *A. belzebul* in forest patches. Although we found
267 howlers in forest patches with varying palm densities, the absence records were concentrated
268 in forest patches with low palm densities and only one of the 10 patches that had over 100
269 palms/ha was not occupied by howlers (Figure 2). The GAM using the LOESS function

revealed a mostly linear relationship between palm density and the occurrence of *A. belzebul* in our sample.

Discussion

We found that patch area is the best predictor for the occurrence of *A. belzebul* in forest patches of the savannas of Amapá. Additionally, while the extent of flooded forest (measured as the density of flooded area palms) increased the probability of occurrence, *A. belzebul* tolerated variation in the structural configurations of forest patches. We suggest that the effect of flooded forests on the occurrence of *A. belzebul* is related to the potential of this habitat to show peaks in fruit production during lean periods in the dry portions of small forest patches (<100 ha) (Ahumada et al., 1998; Haugaasen & Peres, 2005).

Vegetation structure

Alouatta belzebul tolerated the variation in the structural configurations of forest patches we found in our sample. Howler monkeys are known to tolerate variation in the structure of the forests they occupy, including different degrees of disturbance, due to their dietary flexibility (Bicca-Marques, 2003; Bicca-Marques et al., 2020). They cope with food scarcity by adjusting their diet to the species available, and relying on the consumption of leaves, a relatively stable and abundant source of food in forests when fruits are scarce (Bicca-Marques, 2003).

Although most vegetation structure variables were not useful in predicting the occurrence of *A. belzebul* in our sample, we do not rule out the inherent dependence on forest structure for the survival of this arboreal primate. Such variables may have a greater influence on population parameters, such as density and demography, than on distribution. For example, the abundance of *A. palliata* in fragments is positively affected by canopy height, although canopy height does not influence the probability of occurrence (Anzures-Dadda & Manson, 2007).

Indicators of food availability, such as greater abundance and basal area of important food sources or the area of the patch/fragment, are important drivers of the occurrence of *Alouatta* spp. (Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez et al., 2007; Cristóbal-Azkarate, Veà, Asensio, & Rodríguez-Luna, 2005). In an extreme example, *Alouatta pigra* can maintain a population structure in eucalyptus plantations similar to that of populations in native forests, thanks to the food found in vines, vegetation growing below the eucalyptus, and secondary vegetation in adjacent areas (Bonilla-Sánchez, Serio-Silva, Pozo-Montuy, & Chapman, 2012). In other words, howlers may survive in a forest with a structure very different from that of native forests if there is food available.

Patch attributes

Forest patch area had the strongest effect on the occurrence of *A. belzebul.* Patch area is related to a series of factors that converge for a positive effect of this variable on the probability that primates occur, including resources (food, space), metapopulation dynamics (the probability of colonization and extinction), and genetic diversity. The resource limitations imposed by the reduced size of a forest patch, increase the probability of local extinctions (Rodriguez-Toledo, Mandujano, & García-Orduña, 2003; Silva et al., 2016). The probability of colonization also decreases with the size of the patch (Rodriguez-Toledo et al., 2003). Finally, the loss of genetic variability through inbreeding, genetic drift, and stochastic processes make small populations more vulnerable to environmental changes and diseases (Frankham, Ballou, Briscoe, & Ballou, 2002). Together, these processes contribute to a reduction in the probability that primates occur in smaller patches.

Patch isolation is bound to affect metapopulation dynamics beyond certain thresholds. However, 84% of the forest patches in our sample had isolation distances of less than 200 m, the threshold for fragment occupancy by *A. palliata* in the least fragmented of two landscapes

317 studied in Los Tuxtlas, Mexico (Mandujano & Estrada, 2005). An assessment of the overall
318 connectivity of the landscape would be useful in determining how important patch isolation
319 may be for the metapopulation dynamics of *A. belzebul* in the savannas of Amapá.

320 A positive effect of patch or fragment area on the occurrence of howlers is well
321 documented (Rodriguez-Toledo et al. 2003, Cristóbal-Azkarate et al. 2005, Anzures-Dadda and
322 Manson 2007, Puig-Lagunes et al. 2016 – *A. palliata*, Silva et al. 2017 – *A. guariba clamitans*).
323 One factor potentially related to the higher prevalence of howlers in larger patches is protection
324 against hunting. Howlers are highly sensitive to hunting pressure and this, in turn, is positively
325 and directly related to human access to their area of occurrence (de Thoisy, Renoux, & Julliot,
326 2005). Thus, larger patches where access to the interior is more difficult provide greater
327 protection (Geldmann et al., 2013). However, this relationship is likely more evident for
328 primates in continuous forests, as hunters often go up to 5 km into the forest (de Thoisy et al.,
329 2005), which is enough to cross any of the forest patches in our sample (maximum length <4
330 km). Nevertheless, mammals in larger forests may persist under higher hunting intensities
331 because the population is larger (Silva et al., 2016). Patch area is positively correlated with
332 plant species richness and the basal area of the main plant species that are food sources for
333 howlers (Arroyo-Rodríguez & Mandujano, 2006). In the context of forest patches or fragments,
334 the greater availability of resources in larger patches is probably the main factor behind the
335 positive effect of patch area on the occurrence of primates.

336 ***Flooded area palms***

337 We used the density of flooded area palms (açaís, buritis, and caranãs) to quantify the
338 amount of flooded forest in the forest patches of the savannas of Amapá and observed a positive
339 effect of this variable on the occurrence of *A. belzebul*. Although there is little information
340 available on how *A. belzebul* use flooded forests, a group living in Central Amazon visited the

flooded portions (igapó) of their home range daily during the three months of peak water level, when fruit production was intense in that habitat (Pinto, 2002).

Riparian and flooded forests are amongst the preferred habitats of *A. seniculus* and flooded forests dominated by palm trees are their most used habitat in some regions (Aquino, López, García, & Heymann, 2014; Carretero-Pinzon & Defler, 2019). Studies of primates using flooded forests adjacent to unflooded forests often relate this behavior to the exploitation of food sources in flooded forests, especially fruits (Ahumada et al., 1998; Carretero-Pinzon & Defler, 2019; Pinto, 2002; Stevenson, Quinones, & Ahumada, 2000).

Different factors regulate fruit production in flooded and unflooded forests. While rainfall and irradiance are the main factors correlated with phenological patterns in unflooded forests, seasonal flood pulses are the main factor in flooded forests (Haugaasen & Peres, 2005). These different regulatory mechanisms and differences in the floristic composition may produce divergent patterns in fruit production even in adjacent communities (Ahumada et al., 1998; Defler & Defler, 1996). Unflooded forests have a greater floristic diversity and fruit production overall, but in periods of fruit scarcity, adjacent flooded forests may produce a complementary peak in fruit production that may be key to the survival of frugivorous primates (Ahumada et al., 1998).

Alouatta belzebul is the most frugivorous species of howler monkey, with fruits generally comprising 30-70% of their diet, while other species of howlers rarely exceed 30% (Bicca-Marques, 2003; Coutinho, 2012). Portions of flooded forest in the home range of *Ateles belzebuth* are keystone habitats that provide fruits for these highly frugivorous primates during lean periods and reduce the area they require to survive (Ahumada et al., 1998). The flooded forests in the savannas of Amapá may serve a similar purpose for *A. belzebul*. The positive effects of this habitat as a complementary source of fruits would be especially evident for

365 populations in the savannas of Amapá because of the predominantly small (<100 ha) forest
366 patches in the landscape. However, unflooded forests tend to be the main habitat used by
367 frugivorous primates throughout the year because of their usually greater plant diversity and
368 fruit productivity compared to adjacent flooded forests (Ahumada et al., 1998; Pinto, 2002).

369 Although we found a linear positive relationship between palm density and the probability
370 of occurrence of howlers, it is unlikely that the palms themselves are responsible for this pattern.
371 Instead, we hypothesize that this variable correlates with factors that favor *A. belzebul*.
372 Asynchronous patterns in fruit production between flooded forests and adjacent unflooded
373 forests (Ahumada et al., 1998), and higher leaf turnover (Stevenson et al., 2000) and soil fertility
374 (Peres, 1997) in flooded forests compared with unflooded forests are all potentially correlated
375 with palm density in our sample. Thus, the observed relationship between palm density and *A.*
376 *belzebul* does not imply that a forest patch composed almost entirely of flooded area palms
377 (e.g., isolated açaizais or stands of buriti), which we did not sample in this study, will have a
378 high probability of *A. belzebul* occurrence.

379 ***Implications for conservation***

380 The savannas of Amapá are the least protected region of the state, with only ~9% of the
381 area protected, mostly as areas of multiple-use (Mustin et al., 2017). However, a study has
382 recommended that 30% of the savannas should be protected (Hilário et al., 2017). As the only
383 threatened primate found in this ecosystem, we argue that these potential new protected areas
384 should include areas where *A. belzebul* occurs. Our results suggest that the selection of areas
385 for the conservation of this primate should prioritize regions with a higher mean patch size or
386 a greater prevalence of forest patches larger than 100 ha. Additionally, the selected patches
387 should include mostly unflooded forests but also portions of flooded forests, resulting in an
388 overall density of over 100 flooded area palms per hectare.

389 One of the palm species we studied was the açaí, *E. oleracea*, whose fruits have high
390 socioeconomic value (Queiroz & Machado, 2007). Açaí has been the focus of research and
391 management projects because of its economic importance (Quaresma & Cunha, 2012). The
392 reputation of this forest product can be an opportunity to promote the conservation of *A.*
393 *belzebul* in Amapá. Community management projects for açaizais (areas with high densities of
394 açaí palms mixed with native dicot trees) where *A. belzebul* occurs could be used to disseminate
395 information on the ecological importance of this primate, and on the threats to its survival,
396 leading local communities to value these primates alive (*i.e.* to avoid hunting them).

397 In summary, besides showing that the probability of occurrence is higher in larger habitat
398 patches (a well-established relationship), we found that the habitat configuration (i.e. palm
399 density) is more important than some forest structure attributes in predicting the occurrence of
400 *A. belzebul* in forest patches. Although plant composition is usually more difficult to survey
401 than forest structure, we encourage researchers to include this parameter in future studies
402 investigating predictors of primate occurrence in forest patches, which is important for primate
403 conservation. Further investigations on how *A. belzebul* uses the seasonally flooded forests in
404 the patches they inhabit should clarify the reason why palm density predicts their occurrence in
405 the forest patches in Amazonian savannas.

406

Acknowledgments We thank the local communities for sharing their knowledge and assisting the researchers during the fieldwork. This investigation was funded by The Rufford Foundation (22322-1), the Conservation Leadership Programme (02327917), and Idea Wild. SMS and BRCR are supported by student stipends from CAPES. CAPES (Edital 21/2018) supports RRH, through the National Program for Academic Cooperation in the Amazon (PROCAD-Amazônia, Process no. 88881.314420/2019-01). Additional training was provided by the Post-Graduate

Program in Tropical Biodiversity at the Federal University of Amapá, funded by the PROCAD-Amazônia/CAPES (No. 88887.200472/2018-00). Finally, we thank the anonymous reviewers, whose insightful comments significantly improved this manuscript.

Data availability statement Data available on request from the authors.

407

References

Ahumada, J. A., Stevenson, P. R., & Quiñones, M. J. (1998). Ecological response of spider monkeys to temporal variation in fruit abundance: The importance of flooded forest as a keystone habitat. Primate Conservation, 18, 10–14.

Anzures-Dadda, A., & Manson, R. H. (2007). Patch-and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Animal Conservation, 10(1), 69–76. https://doi.org/10.1111/j.1469-1795.2006.00074.x

Aquino, R., & Bodmer, R. E. (2004). Plantas útiles en la alimentación de primates en la cuenca del Río Samiria, Amazonia Peruana. Neotropical Primates, 12(1), 1–6.

Aquino, R., López, L., García, G., & Heymann, E. W. (2014). Diversity, abundance and habitats of the Primates in the Río Curaray Basin, Peruvian Amazonia. Primate Conservation, 28(1), 1–8. https://doi.org/10.1896/052.028.0103

Arroyo-Rodríguez, V., & Dias, P. A. D. (2010). Effects of habitat fragmentation and disturbance on howler monkeys: A review. American Journal of Primatology, 72(1), 1–16. https://doi.org/10.1002/ajp.20753

Arroyo-Rodríguez, V., & Mandujano, S. (2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. International Journal of Primatology, 27(4), 1079–1096. https://doi.org/10.1007/s10764-006-9061-0

Arroyo-Rodríguez, V., Mandujano, S., Benítez-Malvido, J., & Cuende-Fanton, C. (2007). The influence of large tree density on howler monkey (*Alouatta palliata mexicana*) presence in very small rain forest fragments. Biotropica, 39(6), 760–766. https://doi.org/10.1111/j.1744-7429.2007.00330.x

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.40.4. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bicca-Marques, J. C. (2003). How do howler monkeys cope with habitat fragmentation? In Primates in fragments (pp. 283–303). Springer, Boston, MA. https://doi.org/10.1007/978-1-4757-3770-7_18

436 Bicca-Marques, J. C., Chaves, Ó. M., & Hass, G. P. (2020). Howler monkey tolerance to habitat
437 shrinking: Lifetime warranty or death sentence? American Journal of Primatology,
438 82(e23089), 1–9. https://doi.org/10.1002/ajp.23089
439 Bolt, L. M., Schreier, A. L., Russell, D. G., Jacobson, Z. S., Merrigan-Johnson, C., Barton, M. C., &
440 Coggeshall, E. M. C. (2019). Howling on the edge: Mantled howler monkey (*Alouatta*
441 *palliata*) howling behaviour and anthropogenic edge effects in a fragmented tropical rainforest
442 in Costa Rica. Ethology, 125(9), 593–602. https://doi.org/10.1111/eth.12886
443 Bonilla-Sánchez, Y. M., Serio-Silva, J. C., Pozo-Montuy, G., & Chapman, C. A. (2012). Howlers are
444 able to survive in eucalyptus plantations where remnant and regenerating vegetation is
445 available. International Journal of Primatology, 33(1), 233–245.
446 https://doi.org/10.1007/s10764-011-9569-9
447 Calle-Rendón, B. R., Toledo, J. J. de, Mustin, K., & Hilário, R. R. (2020). Drivers of primate richness
448 and occurrence in a naturally patchy landscape in the Brazilian Amazon. Biodiversity and
449 Conservation. https://doi.org/10.1007/s10531-020-02028-z
450 Carretero-Pinzon, X., & Defler, T. R. (2019). Primates and flooded forest in the Colombian Llanos. In
451 K. Nowak, A. A. Barnett, & I. Matsuda (Series Eds.), Primates in flooded habitats: Ecology
452 and conservation (pp. 153–162). Cambridge: Cambridge University Press.
453 Coutinho, L. A. (2012). Variação sazonal e longitudinal na Ecologia do guariba-de-mãos-ruivas,
454 *Alouatta belzebul* (Primates, Atelidae), na Fazenda Pacatuba, Paraíba (Dissertation).
455 Universidade Federal de Sergipe.
456 Cristóbal-Azkarate, J., Veà, J. J., Asensio, N., & Rodríguez-Luna, E. (2005). Biogeographical and
457 floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata*
458 *mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. American Journal of Primatology,
459 67(2), 209–222. https://doi.org/10.1002/ajp.20178
460 de Thoisy, B., Renoux, F., & Julliot, C. (2005). Hunting in northern French Guiana and its impact on
461 primate communities. Oryx, 39(02). https://doi.org/10.1017/S0030605305000384

462 Defler, T. R., & Defler, S. B. (1996). Diet of a group of *Lagothrix lagothricha lagothricha* in
463 southeastern Colombia. International Journal of Primatology, 17(2), 161–190.
464 https://doi.org/10.1007/BF02735446
465 Dias, P. A. D., Alvarado-Serrano, D., Rangel-Negrín, A., Canales-Espinosa, D., & Cortés-Ortiz, L.
466 (2013). Landscape attributes affecting the natural hybridization of Mexican howler monkeys.
467 In L. K. Marsh & C. A. Chapman (Eds.), Primates in fragments (pp. 423–435). New York,
468 NY: Springer New York. https://doi.org/10.1007/978-1-4614-8839-2_28
469 Estrada, A., & Coates-Estrada, R. (1996). Tropical rain forest fragmentation and wild populations of
470 primates at Los Tuxtlas, Mexico. International Journal of Primatology, 17(5), 759–783.
471 Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: A
472 synthesis. Global Ecology and Biogeography, 16(3), 265–280. https://doi.org/10.1111/j.1466-
473 8238.2007.00287.x
474 Fox, J., & Weisberg, S. (2011). An R companion to applied regression. Thousand Oaks, CA: Sage
475 Publications. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion
476 Frankham, R., Ballou, S. E. J. D., Briscoe, D. A., & Ballou, J. D. (2002). Introduction to conservation
477 genetics. Cambridge: Cambridge university press.
478 Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., & Burgess, N. D. (2013).
479 Effectiveness of terrestrial protected areas in reducing habitat loss and population declines.
480 Biological Conservation, 161, 230–238. https://doi.org/10.1016/j.biocon.2013.02.018
481 Hastie, T. (2020). Gam: Generalized Additive Models. R package version 1.20. Https://CRAN.R-
482 Project.Org/Package=gam. Retrieved from https://CRAN.R-project.org/package=gam
483 Haugaasen, T., & Peres, C. A. (2005). Primate assemblage structure in amazonian flooded and
484 unflooded forests. American Journal of Primatology, 67(2), 243–258.
485 https://doi.org/10.1002/ajp.20180
486 Hijmans, R. J. (2017). Package 'raster': Geographic data analysis and modeling. R package version
487 2.6-7.
488 Hilário, R. R., Toledo, J. J. de, Mustin, K., Castro, I. J., Costa-Neto, S. V., Kauano, É. E., … Funi, C.
489 (2017). The fate of an Amazonian savanna: Government land-use planning endangers

490 sustainable development in Amapá, the most protected Brazilian state. Tropical Conservation
491 Science, 10, 1–8. https://doi.org/10.1177/1940082917735416
492 Hue, T., Caubet, M., & Moura, A. C. de A. (2017). Howlers and marmosets in Pacatuba: An
493 overcrowded existence in a semi-deciduous Atlantic forest fragment? Mammalia, 81(4).
494 https://doi.org/10.1515/mammalia-2015-0167
495 IBGE. (2017b). Banco de dados SIDRA. Senso Agropecuário [SIDRA database Agricultural census].
496 Retrieved from http://www.sidra.ibge.gov.br/bda/tabela/listabl.asp?c=1612&z=&o=
497 IBGE. (2017a). Panorama das unidades federativas com base no censo demográfico de 2010. V4.3.8.5.
498 Retrieved from https://cidades.ibge.gov.br/brasil/ap
499 IEPA. (2008). Macrodiagnóstico do estado do Amapá: Primeira aproximação do ZEE/ Equipe Técnica
500 do ZEE - AP (3rd ed.). Macapá, AP: IEPA.
501 Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger
502 climate classification updated. Meteorologische Zeitschrift, 15(3), 259–263.
503 https://doi.org/10.1127/0941-2948/2006/0130
504 Mandujano, S., Escobedo-Morales, L. A., & Palacios-Silva, R. (2004). Movements of *Alouatta*
505 *palliata* among forest fragments in Los Tuxtlas, Mexico. Neotropical Primates, 12(3), 126–
506 131. https://doi.org/10.1896/1413-4705.12.3.126
507 Mandujano, S., & Estrada, A. (2005). Detection of area thresholds and isolation distance for forest
508 fragment occupation by howler monkeys, *Alouatta palliata*, in Los Tuxtlas, Mexico. 12.
509 Montenegro, M. M. V., Carvalho, A., Cortes-Ortíz, L., Fialho, M. de S., Jerusalinsky, L., Melo, F. R.,
510 … Veiga, L. M. (2019). *Alouatta belzebul*. IUCN Red List of Threatened Species 2019,
511 e.T39957A17925370. https://dx.doi.org/10.2305/IUCN.UK.2019-
512 3.RLTS.T39957A17925370.en
513 Mustin, K., Carvalho, W. D., Hilário, R. R., Costa-Neto, S. V., Silva, C., Vasconcelos, I. M., …
514 Mendes-Junior, R. N. (2017). Biodiversity, threats and conservation challenges in the Cerrado
515 of Amapá, an Amazonian savanna. Nature Conservation, 22, 107.
516 https://doi.org/10.3897/natureconservation.22.13823

517 Pavelka, M. S. M., & Knopff, K. H. (2004). Diet and activity in black howler monkeys (*Alouatta*
518 *pigra*) in southern Belize: Does degree of frugivory influence activity level? Primates, 45(2),
519 105–111. https://doi.org/10.1007/s10329-003-0072-6
520 Pebesma, E. J. (2004). Multivariable geostatistics in S: the gstat package. Computers & Geosciences,
521 30(7), 683–691.
522 Peres, C. A. (1997). Effects of habitat quality and hunting pressure on arboreal folivore densities in
523 neotropical forests: A case study of howler monkeys (*Alouatta* spp.). Folia Primatologica,
524 68(3–5), 199–222.
525 Pinto, L. P. (2002). Dieta, padrão de atividades e área de vida de *Alouatta belzebul discolor* (Primates,
526 Atelidae) em Paranaíta, Norte do Mato Grosso (Dissertation). Universidade Estadual de
527 Campinas, Campinas, SP.
528 Pozo-Montuy, G., & Serio-Silva, J. C. (2007). Movement and resource use by a group of *Alouatta*
529 *pigra* in a forest fragment in Balancán, México. Primates, 48(2), 102–107.
530 https://doi.org/10.1007/s10329-006-0026-x
531 Puig-Lagunes, Á. A., Canales-Espinosa, D., Rangel-Negrín, A., & Dias, P. A. D. (2016). The
532 influence of spatial attributes on fragment occupancy and population structure in the Mexican
533 mantled howler (*Alouatta palliata mexicana*). International Journal of Primatology, 37(6),
534 656–670. https://doi.org/10.1007/s10764-016-9930-0
535 Quaresma, S. M., & Cunha, E. B. da. (2012). Manejo de açaizais, como prática de gestão e educação
536 ambiental: Um estudo de caso da comunidade de Franco Grande do Bailique/Amapá. Revista
537 Meio Ambiente e Sustentabilidade, 2(1), 100–120.
538 Queiroz, J. A. L. de, & Machado, S. D. A. (2007). Estrutura e dinâmica de floresta de várzea no
539 estuário amazônico no estado do Amapá. Floresta, 37(3), 339–352.
540 https://doi.org/10.5380/rf.v37i3.9930
541 Quinn, G. P., & Keough, M. J. (2002). Experimental design and data analysis for biologists.
542 Cambridge University Press.
543 R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R
544 Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

545 Rimbach, R., Link, A., Heistermann, M., Gomez-Posada, C., Galvis, N., & Heymann, E. W. (2013).
546 Effects of logging, hunting, and forest fragment size on physiological stress levels of two
547 sympatric ateline primates in Colombia. Conservation Physiology, 1(1), 1–11.
548 https://doi.org/10.1093/conphys/cot031
549 Rodriguez-Toledo, E. M., Mandujano, S., & García-Orduña, F. (2003). Relationships between forest
550 fragments and howler monkeys (*Alouatta palliata mexicana*) in southern Veracruz, Mexico. In
551 L. K. Marsh (Series Ed.), Primates in fragments: Ecology and conservation (pp. 79–97). New
552 York: Springer.
553 Silva, F. A. da, Canale, G. R., Kierulff, M. C. M., Duarte, G. T., Paglia, A. P., & Bernardo, C. S. S.
554 (2016). Hunting, pet trade, and forest size effects on population viability of a critically
555 endangered Neotropical primate, *Sapajus xanthosternos* (Wied-Neuwied, 1826). American
556 Journal of Primatology, 78(9), 950–960. https://doi.org/10.1002/ajp.22565
557 Silva, A. S. de A. e, Fortes, V. B., & Voltolini, J. C. (2017). Influência da paisagem na presença e
558 abundância do bugio-ruivo *Alouatta guariba clamitans* em fragmentos florestais no sudeste do
559 Brasil. Mastozoología Neotropical, 24(2), 323–331.
560 Stevenson, P. R. (2016). Neotropical primate communities: Effects of disturbance, resource production
561 and forest type heterogeneity. American Journal of Primatology, 78(4), 391–401.
562 https://doi.org/10.1002/ajp.22518
563 Stevenson, P. R., Quinones, M. J., & Ahumada, J. A. (2000). Influence of fruit availability on
564 ecological overlap among four Neotropical Primates at Tinigua National Park, Colombia.
565 Biotropica, 32(3), 533–544. https://doi.org/10.1111/j.1744-7429.2000.tb00499.x
566 Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken with a
567 smartphone. Journal of Vegetation Science, 27(2), 427–435. https://doi.org/10.1111/jvs.12350
568 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models
569 and extensions in ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W,
570 editors. New York, NY: Spring Science and Business Media.
571

572

Table 1. Summary of the values of the predictor variables used in a logistic regression model to assess drivers of the probability of occurrence of *Alouatta belzebul* in forest patches (n=38).

Variable	Mean ± standard deviation	Min - Max
Patch area (ha)	46.71 ± 51.31	1.82 - 228.47
Isolation (m)	85.11 ± 86.25	10 - 288
Proportion of the patch that is seasonally flooded	0.30 ± 0.27	0.00 - 1.00
Forest height (m)	13.33 ± 2.81	8.26 - 20.62
Modified Canopy Cover index‡	0.80 ± 0.04	0.61 - 0.84
DBH (cm)	18.93 ± 2.89	13.77 - 26.11
Density of palms (n/ha)†	86.91 ± 119.08	0.00 - 404.55

573 †Açaís (*Euterpe oleracea*), buritis (*Mauritia flexuosa*) and caranãs (*Mauritiella armata*).
574 ‡Tichý (2016).

575

576

Table 2. Pearson correlation coefficients between parameters of 38* forest patches in the savannas of Amapá. Significant (< 0.05) correlation coefficients are in bold.

Variables	Patch area	Isolation	Flood	Forest height	Canopy cover	Trees DBH	Density of palms
Patch area							
Isolation	-0.14						
Flood†	0.28	-0.26					
Forest height	0.12	-0.03	0.05				
Canopy cover	-0.08	0.17	-0.14	0.15			
Trees DBH	0.03	0.17	-0.04	**0.62**	-0.33		
Density of palms‡	0.18	0.22	0.30	0.28	-0.34	0.31	

577 *We excluded an outlier from the correlation tests with Canopy Cover.

578 † Proportion of the patch that is seasonally flooded.

579 ‡ Açaís (*Euterpe oleracea*), buritis (*Mauritia flexuosa*) and caranãs (*Mauritiella armata*).

580

581

Table 3. Comparison of the five best (lowest AICc) models to predict the probability of occurrence of *A. belzebul* in forest patches in Amazonian savannas.

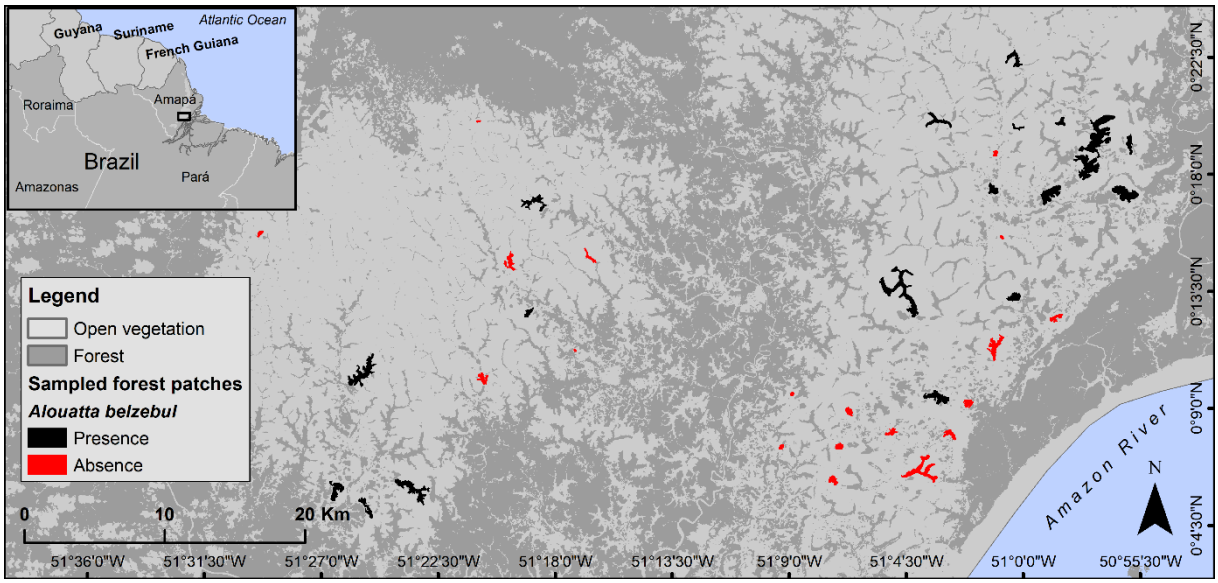
Predictors	df	logLik	AICc	Delta	Weight	R^2
Patch area + Palm density †	3	-13.39	33.49	0	0.24	0.492
Patch area + Palm density + Canopy Cover	4	-13.08	35.38	1.89	0.09	0.503
Patch area + Palm density + Flood‡	4	-13.16	35.52	2.04	0.09	0.501
Patch area + Palm density + Forest height	4	-13.23	35.67	2.18	0.08	0.497
Patch area + Palm density + Isolation	4	-13.38	35.97	2.48	0.07	0.492
Patch area + Palm density + Trees DBH	4	-13.38	35.98	2.49	0.07	0.492

582 †Açaís (*Euterpe oleracea*), buritis (*Mauritia flexuosa*) and caranãs (*Mauritiella armata*).

583 ‡ Proportion of the patch that is seasonally flooded.

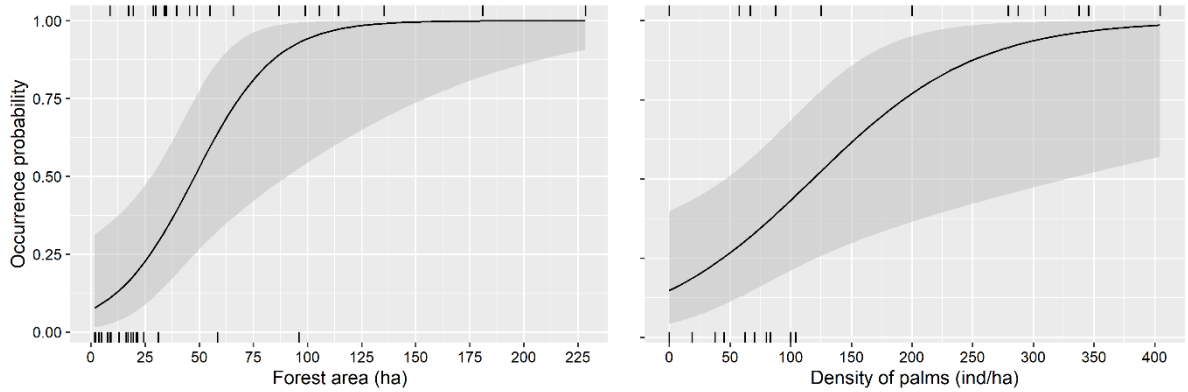
584

585 **Figure 1.** Study region and the location of 38 forest patches where potential predictors of the
586 occurrence of *Alouatta belzebul* were assessed, in the Southeast portion of the savannas of
587 Amapá, northern Brazil.



588

589 **Figure 2.** Logistic models of the effect of (a) area and (b) palm density (*Euterpe oleracea*,
590 *Mauritia flexuosa*, and *Mauritiella armata*) on the probability of *Alouatta belzebul* occurring
591 in forest patches in an Amazonian savanna.



592

593